RETINOMOTOR RHYTHMS IN THE GOLDFISH, CARASSIUS AURATUS [1]

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We had preliminary evidence from histological preparations that the retina of the goldfish, *Carassius auratus*, does show a persistent retino-motor rhythm in prolonged darkness, and we felt that the conclusions of Wigger (1941) stood in need of verification. Wigger (1941) placed the fish in darkness at 1800 hr. and sampled two fish at 2-hour intervals during the first day and at 1200 hr. and 2000 hr. the second day. According to his graph, the cones elongated smoothly to their positions of maximal dark-adaptation by 2200 hr. the first night, contracted sharply to a new position by 2400 hr. and remained there until 0400 hr. Then they contracted sharply to a location intermediate between the light- and dark-adapted positions by 0600 hr. and remained approximately in that position to the end of the experiment. Wigger's results demonstrated that the rhythmic migration of cones in the goldfish retina did not persist in constant darkness after the first 12 hours. He did not distinguish between types of cones.

It is well known that within a species the distances of migration of visual cells may vary considerably as do the thicknesses of the visual cell layers (Ali, 1963; Engström and Rosstrop, 1963) and that single and double cones migrate different distances (Walls, 1942; Nicol, 1965). In repeating these experiments on the goldfish, we followed the separate courses of migration of single and double cones.

MATERIALS AND METHODS

The experiments involved 6 groups of goldfish (mean total length 6.6 ± 0.3 cm.) obtained from Nolt's Ponds, Silver Springs, Pennsylvania.

Group A: 82 fish, conditioned to the natural diel cycle, were placed in the darkroom at sunset, 2036 hr., on June 23, 1965. We fixed samples of 4 fish at 1-hour intervals between 2100 hr. and 0500 hr., and then at sunrise, 0534 hr. Thereafter, we fixed samples of 4 fish at 0800 hr., 1100 hr., 1300 hr., 1500 hr., 1800 hr., and 2036 hr.

Group B: 21 fish, conditioned as in group A, were placed in the darkroom at sunset, July 5, 1965. We fixed three fish at 1300 hr. for 7 consecutive days.

Group C: 12 fish were conditioned for 45 days on an artificial cycle, 12 hr. 20 min. light and 11 hr. 40 min. dark. The light was turned off permanently at 1910 hr. (sunset) on November 19, 1965, and for three consecutive days we fixed two fish at 2400 hr. and 1200 hr.

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Group D: 8 fish, conditioned as in Group A, were placed in the darkroom at sunset, June 13, 1966. We fixed two fish at 0100 hr. and 1300 hr. of the two consecutive days.

Group E: 18 fish, conditioned as in Group A, were placed in the darkroom at sunset on June 27, 1966. We fixed two fish at 1-hour intervals between 2100 hr. and 0500 hr.

Group F: 4 fish, conditioned as in group A, were placed in the darkroom at sunset on July 13, 1966. We fixed two fish at 0300 hr. and 0400 hr.

Light-adapted fish were fixed at 1200 hr. in July and November, 1965.

The fish were maintained in 77.5-liter aquaria equipped with filters and aerators. They were fed daily before noon though not at a regular hour. They were not fed during the experiments. The temperature was 25° ± 1° C.

The fish were fixed in Bouin's fluid in darkness (exclude light-adapted fish) and remained in the fixative at least two hours before the corneas and lenses were removed from the right eyes. The eyes were then dehydrated in an ethyl alcohol series, cleared in xylene, and embedded in paraffin with 1% beeswax.

In group C, radial and serial tangential sections were cut from a sector of retina 2 mm. square, located 1 mm. ventral to the optic nerve. In all other groups, sections were taken from the entire eye through the plane of the optic nerve on a dorso-ventral axis. All sections were cut at 5 or 10 μ and stained with Harris's haematoxylin and eosin. In order to expose the cones for accurate identification and measurement, some sections were bleached with the potassium permanganate-sodium bisulfite method, and stained with 3% ferric chloride and eosin.

The interpretation of the behavior of the retina was based upon the following measurements from each eye:

Group A: 5 measurements of the thickness of the visual cell layer, the location of the single cones, and the location of both the long and short segments of the double cones, all in a region of the retina 1.2 mm. ventral to the optic nerve. The visual cell layer was defined as the distance between the ELM (external limiting membrane) and the lamina basalis. The location of the cones was represented by the distance from the ELM to the distal end of the cone ellipsoid. All measurements were made with an ocular micrometer.

Group B: All measurements made as in group A.

Group C: Radial sections measured as in group A. On the serial tangential sections, using a Whipple-Hauser ocular micrometer, we counted the numbers of single and double cones in an area 670 μ square in each section beginning at the ELM and progressing to the lamina basalis. The distance between elements in successive sections was represented by the thickness of the sections, 5 μ.

Groups D, E, and F: The measurements were made as in group A except that 10 measurements were made rather than 5.

For final comparisons the measurements were converted to RP values (location of visual cell/thickness of visual cell layer × 100) described by Engström and Rosstrop (1963).

RESULTS

All graphs of double cones from radial sections represent the measurements on the long segment which had a mean length of about 3 μ greater than the short seg-

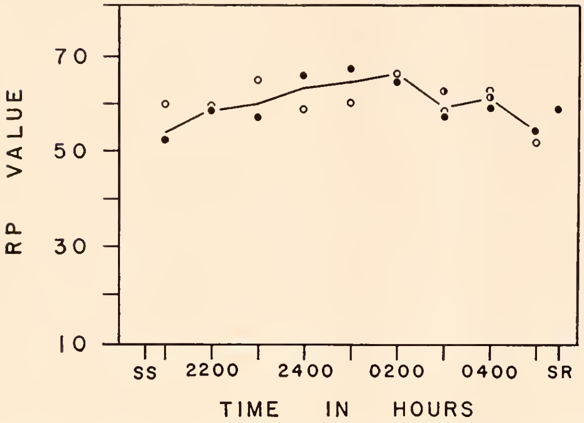

FIGURE 1. Pattern of migration of double cones during first night of darkness. ● Group A, ○ group E, and ◑ group F. SS = sunset, SR = expected sunrise, — = mean values.

ments. There was no change in the difference between the lengths of short and long segments for eyes fixed at different times. The patterns of photomechanical changes during the course of the first night are shown for double cones in Figure 1, and for single cones in Figure 2. Each graph is a composite of results from experimental groups A, E, and F. The points on the graph within a group are not based upon equal numbers of fish because some of the eyes did not produce useful histological sections. In Figure 1, the points for group A at 0100 hr., 0200 hr., and 0400 hr. represent three fish; all other points represent 4 fish. The point for group E at 2100 hr. represents one fish and all other points represent two fish. Each point for group F represents two fish. In Figure 2, the points for group A at 0100 hr. and 0400 hr. represent three fish; 0200 hr., two fish; all other points 4 fish. In group E, the point at 2100 hr. represents one fish, and all other points represent two fish. Each point for group F represents two fish.

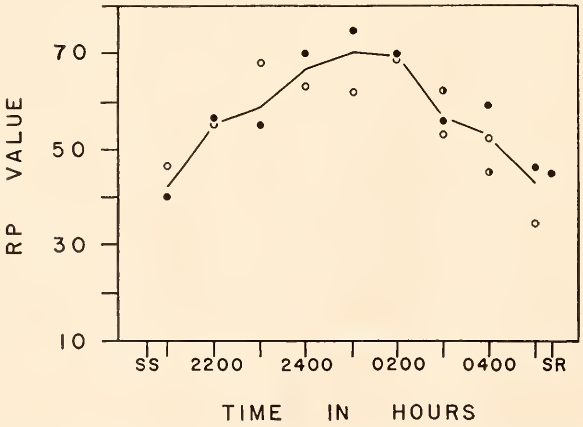

FIGURE 2. Pattern of migration of single cones during first night of darkness. ● Group A, ○ group E, and ◑ group F. SS = sunset, SR = expected sunrise, — = mean values.

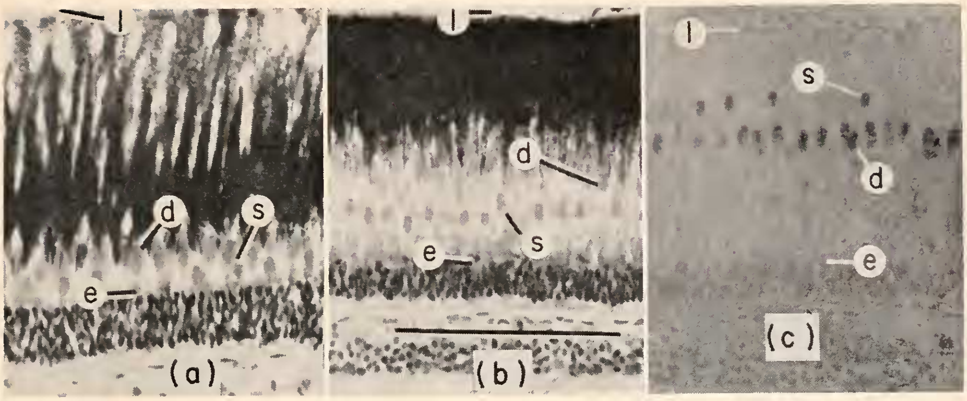

FIGURE 3. Photomicrographs of radial sections showing retinas in different states of adaptation. (a) Light-adapted, $10\ \mu$, H&E. (b) Noon dark-adapted after 17 hours in darkness, $10\ \mu$, H&E. (c) Midnight dark-adapted after 5 hours in darkness, pigment bleached; $5\ \mu$, ferric chloride and eosin. The bar in (b) represents $100\ \mu$. e = external limiting membrane, l = lamina basalis, s = single cones, and d = double cones. 450 ×.

The cones migrated through a cycle of positions during the course of the night, but in each group of fish they followed an irregular and unique course with maximal extensions occurring at different times in the night. Between 2100 hr. and 0200 hr., the corresponding points of groups A and E almost always deviated in opposite directions. The plot of the mean within that interval was relatively smooth. Between 0200 hr. and 0500 hr., the fluctuations in groups A and E followed parallel courses and both exhibited a prominent positive shift in the slope

TABLE I

Mean RP values of double cones during the first 24 hours in darkness, based upon radial sections. Sunset was at 2036 hr. and the expected sunrise was 0534 hr. Plus and minus values represent one standard deviation. The p values are based upon Student's t-test between successive time periods

Groups	Time	Number of fish	RP value	p
A, E, F	2100	5	53.6 ± 5.1	
	2200	6	59.2 ± 2.5	$> .05$
	2300	6	59.5 ± 4.8	n. s.
	2400	6	63.5 ± 5.8	n. s.
	0100	5	64.4 ± 4.1	n. s.
	0200	5	65.6 ± 3.4	n. s.
	0300	8	59.1 ± 6.9	n. s.
	0400	7	61.1 ± 4.4	n. s.
	0500	6	54.2 ± 2.9	$> .01$
A only	0534	4	59.3 ± 7.3	n. s.
	0800	3	45.1 ± 1.1	$> .05$
	1100	3	49.0 ± 3.6	n. s.
	1300	4	50.2 ± 3.9	n. s.
	1500	4	53.8 ± 6.4	n. s.
	1800	4	53.7 ± 8.4	n. s.
	2037	4	50.0 ± 3.8	n. s.

TABLE II

Mean RP values of single cones during the first 24 hours in darkness, based upon radial sections. Sunset was at 2036 hr. and the expected sunrise was 0534 hr. Plus and minus values represent one standard deviation. The p values are based upon Student's t-test between successive time periods

Groups	Time	Number of fish	RP value	*p*
A, E, F	2100	5	41.2 ± 8.0	
	2200	6	57.6 ± 6.8	> .01
	2300	6	59.3 ± 7.3	n. s.
	2400	6	67.8 ± 8.1	> .05
	0100	5	69.9 ± 7.8	n. s.
	0200	4	69.8 ± 3.0	n. s.
	0300	8	57.0 ± 6.7	> .01
	0400	7	53.2 ± 6.9	n. s.
	0500	6	42.8 ± 7.3	> .05
A only	0534	4	46.4 ± 13.0	n. s.
	0800	3	30.8 ± 3.7	n. s.
	1100	3	38.6 ± 0.7	> .05
	1300	4	31.3 ± 7.8	n. s.
	1500	4	32.6 ± 3.9	n. s.
	1800	4	30.7 ± 4.3	n. s.
	2037	4	30.3 ± 4.6	n. s.

of the curve between 0300 hr. and 0400 hr. The slope of the curve in that interval for group F was negative.

The single cones showed a greater photomechanical shift than the double cones. The photomicrographs in Figure 3 show that the distal margins of the ellipsoids of single cones were nearer the ELM in the 1300 hr. retina and farther from the ELM in the 0100 hr. retina than the double cones. The relative fluctuations between points in the graphs of single and double cones were about equal (Figs. 1 and 2), but the single and double cones may have shown some independent behavior.

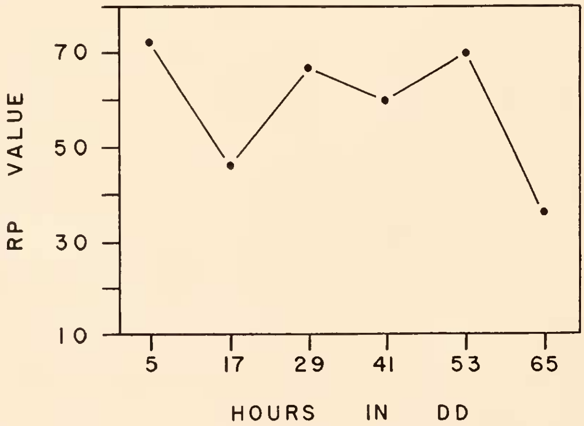

FIGURE 4. Rhythmic shift of positions of double cones based upon serial tangential sections. Group C.

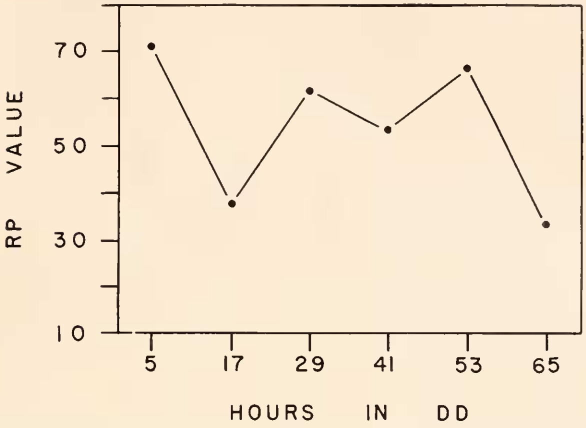

FIGURE 5. Rhythmic shift of positions of single cones based upon serial tangential sections. Group C.

Note in Figure 1 that only three of the points for group A lie above those of group E, while in Figure 2, 7 of the points for group A lie above those of group E.

Tables I and II summarize the combined statistical data for groups A, E and F. As shown by the probability values derived from Student's t-test, there were significant differences between the adjacent points from 2100 hr. to 2200 hr., 2300 hr. to 2400 hr., 0200 hr. to 0300 hr., and 0400 hr. to 0500 hr. The significant differences practically alternated with insignificant differences. The data for group A show that both single and double cones continued to contract beyond the time of expected sunrise. The RP values reached a minimum at 0800 hr. and fluctuated around that value through the remainder of the day.

Both single and double cones showed a persistent photomechanical rhythm in constant darkness. This was first demonstrated by group C (Figs. 4 and 5) in which the results were based upon serial tangential sections. Note that the

TABLE III

Mean RP values of double cones through 65 hours in darkness, based upon serial tangential sections. The eye at 0 hr. was light-adapted. Sections progress from the ELM toward the lamina basalis. Plus and minus values represent one standard deviation

Hours in DD	Fish number	Serial section sequence																			RP value
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
0	1	0	34	50	21																20.9 ± 5
5	2	0	0	0	0	0	0	0	0	0	2	17	29	18							82.5 ± 6
5	3	0	0	0	0	0	0	13	25	35	26										61.3 ± 7
17	4	0	0	0	0	0	0	3	5	2	11	19	17	8							53.4 ± 8
17	5	0	0	0	4	7	10	12	17	20	14										38.0 ± 9
29	6	0	0	0	0	0	0	0	0	0	1	1	13	29	30	19					70.4 ± 6
29	7	0	0	0	0	0	0	0	0	0	0	1	5	17	38	29	21	3			66.2 ± 17
41	8	0	0	1	1	0	0	7	17	18	20	16	5								54.4 ± 10
41	9	0	0	0	0	0	2	0	2	1	0	8	19	17	17	17	3	4			64.0 ± 10
53	10	0	0	0	0	0	0	0	0	0	0	0	0	6	12	26	46	37	21	1	72.5 ± 6
53	11	0	0	0	0	0	0	0	0	0	0	2	20	34	27	9	1				69.2 ± 9
65	12	0	2	10	17	17	19	17	8	0	1										24.9 ± 8
65	13	0	0	0	6	11	19	17	10	5	2										42.2 ± 10

TABLE IV

Mean RP values of single cones through 65 hours in darkness, based upon serial tangential sections. The eye at 0 hr. was light-adapted. Sections progress from the ELM toward the lamina basalis. Plus and minus values represent one standard deviation

Hours in DD	Fish number	Serial section sequence																				RP value
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
0	1	4	45	24	3																	19.8 ± 4
5	2	0	0	0	0	0	0	0	1	4	7	15	22	9	1							78.7 ± 9
5	3	0	0	0	3	3	5	6	20	29	27	1										62.7 ±13
17	4	0	0	3	25	25	9	19	20	23	23	25	26	29	9	4	5					45.5 ±19
17	5	2	6	7	12	13	4	11	16	18	10	2										32.0 ±13
29	6	0	0	0	0	1	2	1	6	1	2	5	11	16	15	15	1					63.2 ±14
29	7	0	0	0	0	1	3	4	1	1	0	0	7	33	25	13	11	1				60.4 ±10
41	8	0	0	6	14	14	6	5	5	9	17	18	11	1								46.8 ±14
41	9	0	1	1	5	9	11	10	4	5	10	12	13	20	29	23	22	15				58.6 ±19
53	10	0	0	0	0	0	1	2	4	4	8	16	7	15	13	16	12	22	26	8	1	65.2 ±15
53	11	0	0	0	0	0	0	5	2	4	8	12	15	12	13	3						66.4 ±12
65	12	0	13	15	9	15	14	15	19	13	4											26.6 ±11
65	13	0	3	10	13	17	12	17	11	8	1											36.9 ±11

maximal RP values occurred on the first night. After the first night, the cones did not migrate the full distances. Note also that on the first night the maximal extension of single cones exceeded that of the double cones, and that subsequently the single cones did not extend as far as the double cones. In the statistical summary of group C (Tables III and IV), the data for fish numbered 4 through 10 strongly suggested the existence of two populations of single cones. (We did not attempt to distinguish between types of single cones.)

The persistent rhythm in the cones was again demonstrated by group D (Figs. 6 and 7). Although the data for group A were incomplete for these purposes, they were included in the figures with the broken line suggesting the location of the point that is missing at 29 hr.

During 8 days in darkness, as shown by eyes fixed at 1300 hr. (Table V), the cones remained in the intermediate positions corresponding to the positions of the

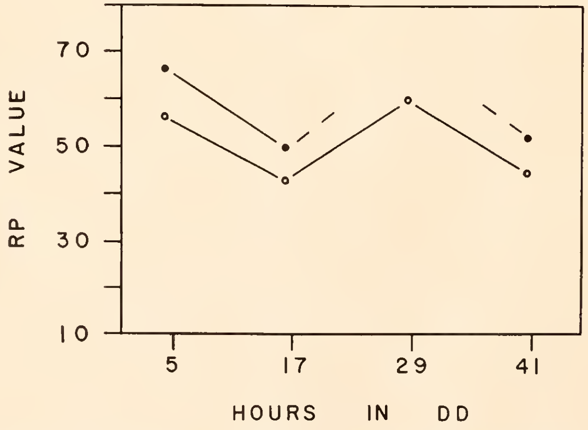

FIGURE 6. Rhythmic shift of positions of double cones based upon radial sections. ● Group A ; ○ group D. Note group A no sample taken at 29 hours.

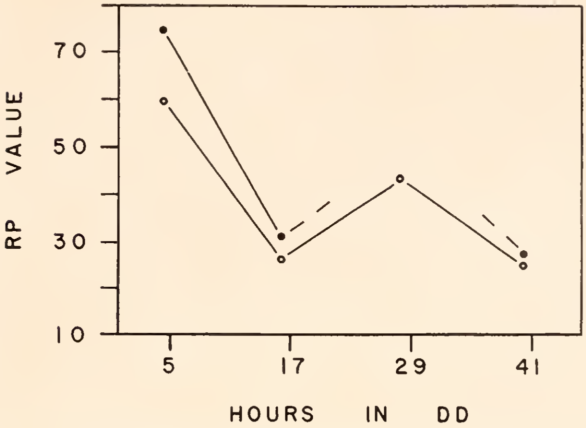

FIGURE 7. Rhythmic shift of positions of single cones based upon radial sections. ● Group A, ○ group D. Note group A no sample taken at 29 hours.

first two or three days. The RP values became consistently smaller for the single cones after the fourth day, but varied up and down for the double cones.

DISCUSSION

Although the retinas of different goldfish under the same conditions showed some marked variations, mean values based upon two fish for each sampling period adequately demonstrated the persistent circadian rhythm in the cones. There may be no statistically significant differences between consecutive points based upon small samples, but the probability of generating a cyclical function by chance is so small that there is little doubt of the validity of the rhythm in the goldfish. If we assumed a normal distribution for the variations between fish, the chance that the values for two fish would both fall either above or below the center of the distribution would be 1/4. The probability of getting the cycle over three days with

TABLE V

Mean RP values of single and double cones at 1300 hr. during 8 consecutive days in darkness. Plus and minus values represent one standard deviation

Day	Number of fish	RP value	
		Single cones	Double cones
1	4	31.3 ± 7.8	50.2 ± 3.9
2	2	28.3 ± 2.7	51.2 ± 0.5
3	3	33.9 ± 4.5	57.2 ± 3.7
4	1	30.6	59.5
5	1	29.2	46.9
6	2	22.8 ± 1.1	53.1 ± 3.6
7	1	19.2	31.7
8	2	20.1 ± 8.9	53.6 ± 6.5

12 fish would be 1/4096, and over two days with 8 fish it would be 1/256. The reproducibility of the rhythm with different lots of fish further supported its validity.

Using small samples, one could not predict the exact time of occurrence of maximal amplitudes in the retinomotor cycle as shown by the graphs in Figures 1 and 2, but the ease of obtaining the cycle indicated that the variations through the middle of the night did not generally overlap with those of the day. The rhythms were demonstrated by small samples collected at the mid-points of the nocturnal and diurnal segments of the cycle. In fact, had only one fish been represented in each sample, a cyclical function would have been obtained most of the time. In only one of 12 fish, no. 9 (Tables III and IV), did the mean positions of the cones deviate sufficiently to obscure the existence of a rhythm. The failure of Wigger (1941) to observe a persistent retinomotor rhythm in the goldfish is inexplicable.

We do not know why the values for group D were consistently lower than those of group A (Figs. 6 and 7). The fish were the same size, obtained at the same time of year, and treated in the same way, but did represent different years. We do not know whether the fish had different experiences prior to our purchasing them. It is well established from work on other organisms that the circadian rhythms are sensitive to a wide range of factors (Aschoff, 1965).

None of the cycles in this study or in the literature represent an individual fish. They represent small samples and the variations show that the results from small samples have limited comparative value. They also represent estimates of the mean values for the populations from which the samples were drawn, but it could be misleading to generalize about population values from small samples. Wigger (1941) paid particular attention to the fact that the cones in darkness became maximally extended before 2400 hr. and contracted about half the distance to a stable position between 2400 hr. and 0400 hr. before contracting farther. Our results (Figs. 1 and 2) illustrate that the time of maximum extension of the cones for any individual or small number of fish might occur at any time from 2300 hr. to 0300 hr. It would be interesting to be able to follow the course of migration of cones in a single fish.

It is important to note that Wigger (1941) sampled fish every two hours while we sampled fish every hour. If the graphs in Figures 1 and 2 were redrawn connecting points at two-hour intervals beginning at 2200 hr., the conspicuous fluctuations would disappear and the curves would become relatively smooth and symmetrical and would contradict our results as well as those of Wigger (1941). It is apparent that the shape of the curve is a function of the sampling interval.

The mean values of the graphs in Figures 1 and 2 suggest a change in the slope of the curve at 0300 hr. This change would be attributed to groups A and E, but the contrary results of group F suggest that the deflections of groups A and E were caused by chance. Further work would be required to determine the mean values and the nature of the variations for the population.

Engström (1960) described two types of single cones in the light-adapted goldfish retina and stated that the shorter type had no myoid process. This means that the shorter cones would not migrate during adaptive changes in the retina. We do not doubt the occurrence of two types of single cones, but a comparison of measurements from light-adapted (no. 1) and dark-adapted (nos. 2 and 3) fish in Table IV shows that all single cones migrated an average of 50 RP units, which means that all cones possessed myoid processes. We think that any interpretation of migratory capacities of visual cells should be based on a comparison of light- and dark-adapted eyes.

Our studies have shown that to obtain an eye in a state of maximal dark-adaptation, one must choose eyes during the first night of darkness. Thereafter, though the circadian rhythm would give a more dark-adapted eye at night than during noon darkness, the RP values would be distinctly lower than they would be on the first night. Arey and Mundt (1941) stated that the rhythm in the black bullhead, *Ameiurus nebulosus,* persisted through 4 days of constant darkness, the limit of their experiment.

Engström and Rosstrop (1963) interpreted this as a general guideline for experimental designs. To assure that the eyes of the roach, *Leuciscus rutilus,* were totally dark-adapted and free from the influence of a rhythm, they held the fish in darkness for 4 days before initiating studies on retinal adaptation at low levels of illumination. They illustrated the retina of a roach exposed to 10^{-6} ft. c. and stated (p. 155) that, "A histological comparison between eyes from '. . . 10^{-6} ft. c. . . .' and the totally dark-adapted ones does not reveal any noticeable differences." The dark-adapted eye was not identified, but was presumably one that had been in darkness for 4 days. They also did not state the time of fixing the eye. Their illustration of the retina of the roach looks like a 1300 hr. dark-adapted goldfish retina and not like a 2400 hr. dark-adapted retina. See Figure 3 and Tables III and IV for the relative positions of single and double cones in the 1200 hr. and 2400 hr. goldfish retinas. We think that the retina of the roach, after 4 days in darkness, was exhibiting a persistent rhythm. The question on the longevity of the persistent retinomotor rhythm in fishes has not been answered. At the end of three days, it was well defined in the goldfish, and the conditions of the retinas at 1300 hr. over a period of 8 days of darkness suggest that the rhythm was persisting. At least, the retina was remaining in an intermediate condition, not a dark-adapted condition.

Generalizations on the presence or absence of persistent retinomotor rhythms in fishes appear to be based on inadequate factual support. Von Studnitz (1952), citing the appropriate literature, mentioned two species in the discussion of rhythms, the black bullhead and the goldfish. Since, according to Wigger (1941) the goldfish did not show a persistent rhythm, the sole evidence for such a rhythm rested on the bullhead. Yet, Ali (1961) cited von Studnitz (1952) for the statement that rhythms occur in certain fishes. Engström and Rosstrop (1963) cited von Studnitz (1940) as the authority for the statement that persistent retinomotor rhythms are not general among fishes. There has not been sufficient study to support any wide generalization on persistent retinomotor rhythm in fishes, but the following quotation (p. 357) from Welsh and Osborn (1937) indicates that such rhythms may be widespread: "Several species (not named in the paper) other than *Ameiurus* were treated. . . . Not enough individual fishes were employed, however, to yield quantitative results, but without question, the phenomenon is fairly widespread."

SUMMARY

1. The goldfish retina shows a persistent circadian rhythm. In constant darkness for three days, the cones continued to shift positions in synchrony with the

diel cycle. The amplitude of the shift decreased after the first night. A maximally dark-adapted retina was obtained only on the first night.

2. Individual fish showed considerable variation in the time of occurrence of maximal dark-adaptation. This condition might be attained at any time between 2300 hr. and 0200 hr. The mean values for all fish suggested that the curve of progress of dark-adaptation for the population would be symmetrical with the maximal dark-adapted condition occurring at mid-night.

3. The single and double cones showed some characteristic differences in their behaviors. All cones migrated, but the relative excursions of single and double cones changed after the first night. The migratory patterns suggested the existence of two kinds of single cones.

4. The longevity of persistent rhythms in fish retinas is not known, but the assumption that it ceases after 4 days is based upon misinterpretation of a statement by Arey and Mundt (1941) about the black bullhead.

5. After 8 days in darkness the retina at 1300 hr. was in an intermediate state, not dark-adapted. If anything it had drifted toward the light-adapted state.

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